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BEHAVIORAL SELECTION BY CONSEQUENCES

SELEÇÃO COMPORTAMENTAL POR CONSEQUÊNCIAS

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RESUMO

Como um processo, seleção consiste em (a) variação de características, (b) interação diferencial com o ambiente com base na variação de características e (c) replicação diferencial de características benéficas, adaptativas, na forma de sua transmissão para, e expressão em, futuras gerações de uma população. A análise do comportamento sugere que a seleção se aplica à análise do comportamento de um organismo, tanto quanto a uma análise de sua morfologia e da origem da espécie. Os três níveis aos quais analistas do comportamento aplicam o princípio de seleção são (a) filogenético, para o desenvolvimento de um repertório inato em uma espécie; (b) ontogenético, para o desenvolvimento de um repertório operante durante o tempo de vida de um organismo individual; e (c) cultural, para o desenvolvimento de práticas culturais em um grupo social. Grande parte da psicologia tradicional está comprometida em postular causas antecedentes do comportamento, particularmente quando tais causas são assumidas como sendo mentais. Este artigo argumenta que uma ciência do comportamento está bem servida ao dispensar interesses em causas mentais antecedentes, em favor da seleção por consequências como modo causal.

Palavras-chave: B. F. Skinner, análise do comportamento, Charles Darwin, evolução, seleção por consequências

ABSTRACT

Selection as a process consists of (a) variation of traits, (b) differential interaction with the environment on the basis of the variation of traits, and (c) differential replication of beneficial, adaptive traits in the form of their transmission to and expression in future generations of a population. Behavior analysts suggest selection applies to the analysis of an organism's behavior just as much as to an analysis of its morphology and the origin of species. The three levels at which behavior analysts apply the principle of selection are (a) phylogenic, for the development of an innate repertoire in a species; (b) ontogenic, for the development of an operant repertoire in the lifetime of an individual organism; and (c) cultural, for the development of cultural practices in a social group. Much of traditional psychology is committed to postulating antecedent causes of behavior, particularly where those causes are assumed to be mental. This article argues that a science of behavior is well-served by setting aside concerns with antecedent mental causes in favor of selection by consequences as a causal mode.

Key words: B. F. Skinner, behavior analysis, Charles Darwin, evolution, selection by consequences.

This article is taken from material I developed over the years to help in my own teaching on the topic of selection by consequences in behavior analysis. I offer it here in the hope others will find it useful. In keeping with the instructional goal of the article, references are at a minimum. In addition, both the language and the arguments are more informal than in other articles. If I have fallen short in the execution, I apologize and ask for the reader's tolerance. I can only say the contingencies haven't finished with me yet. Correspondence concerning the article should be addressed to the author at jcm@uwm.edu, or at his home address: 1861 E. Fox Lane; Fox Point, WI 53217; USA.

BEHAVIORAL SELECTION BY CONSEQUENCES

In his landmark book *On the Origin of Species*, Charles Darwin (1859) sought to explain how species might arise, flourish, or become extinct. Foremost among his explanatory principles were *selection* and *evolution*, both derived from a naturalistic orientation to the life sciences. These principles challenged those derived from a religious orientation, such as those assuming that a divine agent created species with an essential set of attributes, and that species arose, flourished, or became extinct through divine intervention. Although selection and evolution were initially controversial, both are now firmly accepted in the scientific community. As the geneticist Theodosius Dobzhansky (1964) famously put it, "Nothing in biology makes sense except in the light of evolution" (p. 449). In anticipation of second half of the present exposition, worth noting also are the related words of the neurobiologist Gordon Shepherd (1988): "Nothing in neurobiology makes sense except in the light of behavior" (pp. 6-7).

In its most general sense, selection consists of an ongoing, repetitive cycle of three features. The first feature is random, intrinsic *variation* in one or more physiological characteristics or properties of the organisms in a population. A synonymous, commonly used term for these characteristics or properties is traits. In today's language, one source of the variation is random, naturally occurring *mutations* when the germ-line cells (eggs, sperm) develop in parents and errors occur as the DNA making up the genes in those cells reproduces or copies itself. The mutations are not due to use or disuse during the lifetime of the parents.

The second feature is *differential interaction* between the characteristics of the organisms and prevailing environmental circumstances. Here, the sense of *interaction* is that of how well an organism's characteristics allow it to meet the demands of the material environment, or how well its characteristics allow it to gain life-maintaining resources given the presence of other organisms, for example, with whom it competes for the same resources. The sense of *differential* is that certain characteristics confer certain adaptive advantages or benefits to the organisms that possess them. The stronger are the advantageous characteristics, the greater is said to be the *fitness* of the organisms. The greater is the fitness of the organisms, the greater is the probability they survive, given the prevailing environmental circumstances. The absence of the relevant characteristics confers no such adaptive advantages. Perhaps the presence of other characteristics is even maladaptive. Organisms without the advantageous characteristics or with maladaptive characteristics are less fit. These organisms cannot compete with more fit organisms for life-maintaining resources. As a result, the probability is low that less fit organisms survive.

The third feature is the *differential replication* of the adaptive, advantageous characteristics in future generations of the population. Here, the surviving organisms - those with the advantageous characteristics - mate and produce offspring. In turn, those offspring mate and produce their own offspring, and so on. The sense of *replication* is that the advantageous characteristics are *transmitted to* and *expressed in* succeeding generations of offspring, and a lineage is established across those generations. The sense of *differential* is that organisms with the advantageous characteristics rather than those without are the ones that contribute descendants to future generations and constitute the lineage. Organisms without the advantageous characteristics, or with maladaptive characteristics, don't survive, don't reproduce, and obviously don't contribute descendants to future generations. Rather, they become extinct.

As a result of the differential replication, the number or percent of organisms in the population with advantageous characteristics progressively increases, while the number or percent of organisms without those characteristics or with disadvantageous characteristics progressively decreases. In this regard, the rate of increase and decrease is a function of the rate of variation in the population.

To be sure, the characteristics of the members of the population continue to mutate over evolutionary time, and further mutations may make the characteristics even more advantageous. If the mutations are indeed more advantageous, they accumulate over time as they are transmitted to and expressed in future generations, consistent with the adaptive benefits they confer to the organisms in those generations. Those organisms are the next step in the lineage. Again, if the mutations are maladaptive, the organisms don't survive, and their characteristics are obviously not replicated.

A final point is that in some cases, organisms with the advantageous characteristics may produce offspring, but these offspring are not fertile. Obviously, these non-fertile offspring do not contribute descendants to future generations of the population, and do not establish a lineage. As an example, male donkeys ordinarily mate with female donkeys. These unions produce more donkeys. Male horses ordinarily mate with female horses. These unions produce more horses. In both cases, the offspring are fertile and contribute to their respective species. In contrast, male donkeys may mate with female horses. These unions produce mules. In this case, offspring are not fertile, do not contribute to a species, and do not establish a lineage.

In summary, the repetitive cycle of (a) variation, (b) differential interaction, and (c) differential replication plays out over the very long periods of evolutionary time. Species emerge when the characteristics of organisms are of service to the organisms as the organisms adapt to the environment, such as when the characteristics allow the organisms to fill an ecological niche that exists at a particular time and place. According to many biologists, these organisms then produce fertile offspring only with like organisms. These fertile offspring mark the establishment of a lineage. In any case, species are not created or designed with a fixed, immutable, and perfect set of characteristics. Species become extinct when environmental circumstances change over time faster than the organisms' characteristics mutate, or when the organisms' originally advantageous characteristics mutate so much that their characteristics are no longer advantageous, given the prevailing environmental circumstances. As suggested above, the fitness of an organism is a matter of how well its characteristics contribute to adaptation based on the prevailing environmental circumstances. Fitness does not imply the existence of some fixed, pre-determined state of perfection, with respect to which the current characteristics of an organism might be an approximation.

SELECTION BY CONSEQUENCES: MORPHOLOGY AND SPECIATION

A scenario about the development of the size and shape of a bird's beak may help to illustrate the cyclic process of selection. Let's begin by supposing that in a given region, say relatively early in evolutionary time, many types of seeds are available upon which a population of birds might feed. Because of the availability of so many types of seeds, beaks of a particular size and shape confer no adaptive advantage when it comes to cracking open and consuming these seeds. As a result, considerable *variation* exists among the members of the population of birds regarding the size and shape of their beaks. Nonetheless, of interest for the present exposition is that with respect to one type of seed—for simplicity, let's call it seed A—birds with beaks of a particular size and shape have an advantage over birds with beaks of other sizes and shapes: The former birds can readily consume seed A, whereas the latter birds cannot. Again, at the start of this scenario, say early in evolutionary time, this advantage is of no particular consequence, as the latter birds can consume other seeds and survive perfectly well.

Next, let's suppose the climate changes in this region. As a result, seed A becomes dominant in the region, and other seeds become less available. The birds with beaks that allow them to consume seed A then have a higher probability of surviving than do the other birds that cannot consume seed A. Their beaks are not better in any absolute sense, but merely more suitable with respect to the environmental circumstances that exist at that time than the beaks of the other birds. This relation illustrates the second feature of selection: *differential interaction* between prevailing environmental circumstances and the characteristics of organisms. Again, if the circumstances differed, for example, because a different seed became dominant, beaks of a different size and shape might be more advantageous.

The third feature of selection is *differential replication*. This feature involves the *transmission of* the advantageous characteristics to future generations of the population and the *expression of* the characteristics in those generations. In other words, over time, the birds with advantageous beaks survive, reproduce, and transmit their characteristics to their offspring, who in turn express these characteristics. Importantly, these birds begin to increase in number, as a consequence of their access to seeds. Perhaps further mutations in the size and shape of the birds' beaks over evolutionary time prove even more adaptive, and the increase is even greater. In contrast, birds with beaks of a different size and shape—a non- or possibly even maladaptive characteristic—begin to decrease in number, as a consequence of their difficulty finding seeds they can consume. In any case, the result is that a population of birds emerges with beaks that tend to be of a particular size and shape.

Darwin was uncertain about the biological mechanism or process for replication, although he did speculate about entities he called "gemmules." Gemmules were very small structures that he imagined to be circulating within an organism's body. As they circulated, they absorbed certain of the organism's characteristics. In turn, the organism's germ-line cells absorbed the gemmules and transmitted them to offspring at conception. The gemmules then circulated in the offspring, who absorbed and expressed the characteristics. Interestingly, Darwin's gemmules allowed for both acquired and innate characteristics to be transmitted from parents and expressed in offspring. The idea that acquired characteristics could be transmitted to and expressed in offspring was based on the ideas of the French biologist Jean Baptiste Lamarck. It was a controversial notion in Darwin's time, but Darwin wanted to acknowledge it. The history of genetics reveals that around this same time, Mendel demonstrated replication was orderly and particulate, although his work remained relatively unknown until it was rediscovered near the end of the 19th century. Further research showed that the characteristics of the parents were sometimes but not always blended in offspring, and acquired characteristics were not replicated in offspring. As the 19th century drew to a close, DeVries and Bateson among others rediscovered and expanded on Mendel's work, laying the foundation for Morgan, Dobzhansky, and the "Grand Synthesis" in the second and third decades of the 20th century, which further identified the principles of the underlying biological mechanism for replication. In mid-20th century, Watson and Crick then identified the molecular mechanism for replication involving the chemical structure of DNA as the basis for the gene.

Thus, organisms that are alive today may be usefully understood as belonging to a lineage of survivors. The lineage developed over evolutionary time, as environmental circumstances selected certain characteristics of the ancestors of the survivors. The characteristics then varied across many generations. As the characteristics varied, the environment selected or rejected the variations. Variations that were adaptive and advantageous contributed to the survival of the ancestors, meaning those ancestors and not others produced fertile offspring with like organisms, and future generations consisted of their descendants. The members of these future generations may be understood as having descended with modification from their ancestors, and the modifications accumulated over succeeding generations. The process is called "natural selection" when the environment selects some organisms to survive, and other organisms to become extinct, based on the presence and absence of certain characteristics. The process is called "sexual selection" when organisms of one sex grant reproductive access to organisms of the other sex because they are receptive to the characteristics (e.g., morphological) of the other sex. These characteristics are then transmitted to and replicated in offspring, becoming prominent in future generations. The process is called "artificial selection" (e.g., "selective breeding") when humans intervene by deliberately mating organisms with (or alternatively, without) certain characteristics to yield future generations with (or alternatively, without) those characteristics. Common examples are farm animals that are bred to lay more eggs or to produce more milk or to yield more meat, or to be more docile as beasts of burden.

In this regard, a common definition of a species among biologists is (a) a reproductively isolated population of organisms with (b) fertile offspring, although this definition is often debated for its limitations. For example, some species reproduce asexually. To be sure, sexual reproduction is advantageous, in that one of the variable characteristics that could be replicated is resistance to disease or pathogens. In addition, suppose an organism of species X mates with an organism of species Y, and its offspring are not fertile. Then, suppose an organism of species Y mates with an organism of species Z, and its offspring are not fertile. What happens when an organism of species X mates with an organism of species Z? The expectation is presumably that the offspring are non-fertile, don't establish a lineage, and are not a species. However, in some cases, the offspring are fertile. Thus, a comprehensive definition of a species awaits.

The concept of a contingency is central to an understanding of selection. In everyday language, the term "contingency" implies an "if ..., then ..." relation, where the relation is conditional or probabilistic, rather than certain or logically necessary. In other words, if particular prior conditions or events obtain, then the probability of a specified outcome or consequence is higher than if those conditions or events don't obtain. Conversely, if those conditions or events don't obtain, then the consequence might be different, or perhaps nothing at all will happen, but at least the probability of the specified consequence is lower than if the conditions or events do obtain. In the case of an organism's morphology and the origin of species, the differential interaction means that the consequence outlined above - survival or extinction - is probabilistically contingent on or probabilistically depends on the relation between the organism's characteristics and prevailing environmental circumstances. Neither survival nor extinction is a necessary outcome based solely on the presence or absence of certain of the organism's characteristics.

Finally, we note that when the environment selects an organism's characteristics, some of those characteristics are the basis or criteria for selection, whereas some characteristics come along with the organism simply because they are part of the organism's endowment. The distinction is "selection for" versus "selection of." The former concerns some specific characteristic as the basis or criterion for selection. The latter concerns the characteristic as a side effect of selection. Consider the previously mentioned population of birds. The birds were selected for the size and shape of their beaks, which afforded the birds the ability to consume seed A. Let's now suppose that the birds who had beaks that allowed them to consume seed A also tended to have red feathers. The two attributes - beaks and feathers - covaried, but only one - their beaks - was the basis for selection. We may most usefully say that there was selection of but not selection for red feathers, in that the colors of the birds' feathers were the side effect of the selection process, rather than the target. As often said, correlation does not imply causation. This distinction is relevant because some attributes of organisms may have participated in the selection process but only as side effects, and subsequent researchers and theorists may have mistakenly identified these attributes as targets.

SELECTION BY CONSEQUENCES: BEHAVIOR

The present thesis is that the principle of selection is as relevant to the development of an organism's behavioral repertoire as it is to the development of an organism's morphology through descent with modification, accumulation of those modifications, and ultimately the origin of species. Indeed, organisms interact with the environment through their behavior. Darwin actually acknowledged the possibility of behavioral evolution in several of his works, such as *On the Origin of Species* (Darwin, 1859), *The Descent of Man* (Darwin, 1871), and *The Expression of the Emotions in Man and Animals* (Darwin, 1872). Emotions were of special concern because Darwin thought they reflected continuity of not only behavioral but also mental evolution particularly well. However, he did not write as extensively about behavioral and mental evolution as he did about morphology and speciation through natural selection.

With regard to behavior, we may identify three levels at which selection by consequences applies: phylogenic, ontogenic, and for humans, cultural. The phylogenic level pertains to the development of species-specific behavior during the lifetime of the species. The ontogenic level pertains to the development and maintenance of more flexible forms of behavior during the lifetime of the individual organism. The cultural level pertains to the development and maintenance of social practices during the lifetime of a group. We can say that both nonhuman and human behavior are selected through interaction with the environment at the phylogenic and ontogenic levels. Recognizing that the matter is much debated, for present purposes let us restrict selection at the cultural level to humans. We may now more closely examine the process of behavioral selection by consequences and the role of contingencies at each of these levels.

BEHAVIORAL SELECTION BY CONSEQUENCES: THE PHYLOGENIC LEVEL

The first level of behavioral selection by consequences is the phylogenic level. Again, this level concerns the selection of innate and species-specific responses through interaction with the environment during the lifetime of the species. Let's assume that in the past, there was a population of organisms. Again, for present purposes the organisms could be either human or nonhuman. Let's further assume that those organisms engaged in responses that were elicited or released by stimuli or features in the environment. Next, let's assume that even though antecedent stimuli elicited or released the responses, some of the responses might still have an adaptive benefit. That is, responses with some characteristics benefitted the organism and ultimately the species because the responses conferred a survival advantage. Some of these benefits may have been direct for the organisms and the species: obtaining food, avoiding predators. Some of these benefits may have been indirect for the species: attracting mates, building nests, caring for offspring. In any case, there was a contingency between the responses and survival. If an organism's responses with respect to the environment possessed the necessary characteristics, then the probability that organism or its offspring survived was higher than if an organism's responses didn't possess those characteristics. If the organism survived, then the probability was higher that it reproduced. If it reproduced, then the probability was higher that its offspring and descendants in future generations were organisms in whom the adaptive, advantageous behavioral characteristics would be replicated. The result was the development of a species with an innate repertoire - the establishment of a behavioral lineage.

For example, organisms whose heart rates increased during encounters with predators were better able to survive because the increased heart rate allowed these organisms to better escape from those predators. Organisms that blinked to gusts of wind that blew around objects dangerous to their eyes were better able to survive because blinking protected their eyes and preserved their eyesight. Organisms that salivated to food were better able to survive because they were better able to swallow and metabolize that food. Organisms that built nests for their offspring, for example, at particular times of the year that were indicated by temperature, sun elevation, and so on, were better able to protect their offspring. Organisms that marketed their availability as potential mates not only through visual appearance but also through vocalization or behavioral ritual to conspecifics that were receptive to such characteristics had a higher probability of reproducing. Hence, their characteristics were differentially transmitted to offspring and differentially expressed in future generations of the population. In contrast, responses with no such advantage may even have been maladaptive. Organisms with maladaptive responses perished. Thus, neither these organisms nor their responses with their characteristics were replicated in the future. Overall, we are talking here about the behavioral counterpart of natural selection. The outcome is that the number of organisms increases or decreases as a function of their behavioral characteristics.

We must add a caveat: This process is beneficial so long as the environment doesn't change appreciably. If the environment does change, then responses wedded to the old environment may no longer be of service, and survival of the organism that persists in engaging in them may be in doubt.

In general terms, we may use the phrase "contingencies of survival" to speak of the behavioral contingencies that selected organisms with certain innate responses at the phylogenic level, through either natural or sexual selection. We may now call these innate responses respondents and certain other forms or patterns of released, species-specific behavior. The contingencies operated over perhaps hundreds of millions of years of evolution during the evolutionary "lifetime" of the species as it evolved. The responses contributed to the survival of the organisms that possessed them. The innate responses were replicated—transmitted to offspring who then expressed them—through the organism's genetics. Again, when considered over evolutionary time, these responses constitute a behavioral lineage. The genetic mechanisms that replicate innate behavior at this level are studied in behavioral genetics. The relations between behavior and environmental circumstances that evoke innate behavior are studied in ethology and comparative psychology.

BEHAVIORAL SELECTION BY CONSEQUENCES: THE ONTOGENIC LEVEL

The second level of behavioral selection by consequences is the ontogenic level. As noted, this level of selection concerns the development and maintenance of responses through interaction with the environment during the lifetime of the individual organism. The responses of principal interest at this level are operants.

In the case of operants, let's assume that during the lifetime of an individual organism, the organism engaged in a randomly varying population of movements. These movements were simply "emitted," rather than elicited or released by specific stimuli or circumstances in the environment, as at the phylogenic level. After all, one of the characteristics of being alive is movement. Perhaps the everyday terms "random" and "spontaneous" may be usefully applied to these variations in movement across time. Overall, this feature is that of *variation*, in the same sense that variations in morphology apply across organisms and time.

Further, let’s assume that movements with some characteristics were followed by certain outcomes, such as certain stimuli or events, that wouldn’t have occurred otherwise. This feature is that of *differential interaction*. Some of these outcomes may well have involved access to life-maintaining resources or avoiding predators, but they may have had other critical outcomes as well.

Next, let’s assume movements that were followed by the aforementioned stimuli or events became more frequent. This increase in frequency is analogous to replication and ultimately the survival of a species. For the purpose of developing a coherent account, let’s now speak of these movements as “responses,” and the conditions, events, or stimuli that are the consequence of the responses as “reinforcers.” Again, some of the reinforcers may well have been related to the biological needs of the organism, and hence its survival. However, not all the reinforcers were related to biological needs. Nevertheless, they still had the effect called reinforcing. Responses with other characteristics that were not followed by these stimuli or events may have been counterproductive. These responses became less frequent, analogous to the extinction of a species. Thus, there was a contingency between the responses and certain stimuli or events in the environment that those responses produced: If a response with the appropriate characteristics was emitted, then the stimuli or events followed as outcomes. The effect was an increase in the frequency of the responses that had these consequences in the setting in which the responses occurred. We may speak of the contingencies that selected these responses, which we may now call operant responses, as “contingencies of reinforcement.” These contingencies operated during the lifetime of the individual organism. The increase in responding that resulted from the contingencies is *differential replication*. The responses were transmitted to the future through the organism’s nervous system, which was modified during the interaction with the environment called reinforcement. The physiological mechanisms at this level according to which consequences modify the behavior that occurs in a given setting—the mechanisms by which reinforcers increase the behavior that produces them, and (to metaphorically adopt the language of genetics) the mechanisms that transmit and express behavior—are studied in behavioral neuroscience: synaptic plasticity and so on. The experiences with environmental events, variables, and relations that select behavior at this level are studied in behavior analysis: lever pressing in rats, key pecking in pigeons, walking and talking in humans.

A process called *shaping* is sometimes responsible for the development of operants. Shaping is analogous to artificial selection. In more formal language, shaping involves differential reinforcement of successive approximations to some desired terminal form of the target behavior. Here, suppose a human delivers a reinforcing consequence after the response of another organism, either human or nonhuman, contingent on that response being successively closer to the desired behavior. Shaping is a contrived process in that it relies on another organism such as a human to deliver the reinforcer, just as artificial selection is a contrived process in that it relies on humans to mate organisms with desired characteristics to produce offspring with those same or perhaps even more desirable characteristics.

In principle, operants might also have a source in elicited or released behavior, as those forms of behavior may have consequences during the immediate lifetime of the orgalater nism. At issue is whether control of the response shifts from the original antecedent elicitation to selection by consequences. That matter is empirical, to be resolved on a case-by-case basis for species, eliciting circumstances, and responses.

The ontogenic level is the level of the lifetime of the individual organism, by virtue of its experiences with the environment. Operant responses are clearly an important component of behavioral selection at this level. Although many forms of operant behavior may develop either within or across species, operant control does not develop for every response of every organism.

Also relevant as perhaps a special case at the ontogenic level are classically conditioned responses, in which an originally neutral stimulus correlated with an unconditioned stimulus comes to elicit a response in the same response system as does the unconditioned stimulus. Although many scenarios are possible, one possibility is that this process originated as a benefit for an organism by preparing it for the impending unconditioned stimulus. The wide variety of stimuli, responses, and organisms that are involved in this process testifies to the various ecological niches that organisms have filled over evolutionary time through the selective action of the environment.

BEHAVIORAL SELECTION BY CONSEQUENCES: THE CULTURAL LEVEL

The third level of behavioral selection by consequences is the cultural level. Again, this level of selection involves the selection of cultural practices through interaction with the environment during the lifetime of a social group. This level applies particularly - perhaps even exclusively - to humans within or across generations, and within or across the same or different groups. Let’s assume that as humans began to live in social groups, the groups developed certain group-based practices that dealt with important aspects of their lives. These practices may have concerned agriculture, irrigation, animal domestication and husbandry, religion, care of natural resources, energy production, disposal of waste, manufacturing, economics, and treatment of others in the group—old, young, infirm, disadvantaged. In short, the concern here is with the ways of doing things that the group as a whole adopts. Let's assume that within or across generations within or across the same or different groups, instances of the practices were distinguished by their randomly varying characteristics. This feature is that of *variation*.

Further, let's assume that some of these practices had a beneficial consequence. That is, practices with some characteristics enabled the group to solve problems or deal effectively with challenges from the environment. These practices contributed to group welfare, and perhaps even to survival of the group. These practices may be viewed as special forms of operant behavior, in the sense that they have consequences, except that they apply across the culture as a whole, rather than to a single organism. Practices with other characteristics did not necessarily contribute to the same extent to the welfare and survival of the group. Some practices may even have been counterproductive, but existed for other reasons, such as by being socially approved even though their material impact was negative. A group who engaged in counterproductive practices was in peril, and it might become extinct unless it changed its ways. Thus, there was a contingency between cultural practices and the ultimate welfare if not survival of the group: If the members of the group engaged in certain practices, then the group as a whole was better able to adapt to its environment and survive. If the members of the group engaged in other practices, then the group as a whole was less able to adapt to its environment and survive. The group might even become extinct. This feature is that of *differential interaction* with respect to the environment.

When the culture survived, its practices were replicated through the interlocking social arrangements of the group and transmitted to future generations through its language. Those practices were then expressed in future generations. This feature is that of *differential replication*.

We may speak of the contingencies that selected these practices, which we may now call a "culture," as "contingencies of cultural evolution." These contingencies operated during the lifetime of the culture. The argument here is that cultural practices are analogous to responses in an organism's repertoire, in that they develop and are maintained relative to environmental circumstances. Cultural practices are not measured on some absolute scale, with the so-called primitive practices of savages and barbarians at the inferior end and the so-called advanced practices of the industrialized, colonizing countries of Europe and North America at the superior end, according to what was called "Social Darwinism." Just as responses in an organism's repertoire are not characterized in such terms, neither are cultural practices. To be sure, many practices are dangerous and counterproductive, just as are other forms of behavior. Nevertheless, the relevant question is how well both individual responses and cultural practices contribute to adaptation and ultimately to the long-term welfare of the culture and even its survival. However, answers to that question are conditional on the relation between the responses and practices, on the one hand, and the prevailing environmental circumstances—particularly outcomes of the responses and practices, on the other. Answers do not follow from assertions of intrinsic intellectual superiority or inferiority of the organisms involved. The mechanisms that replicate cultural practices at this level are studied in social and cultural anthropology.

SUMMARY AND CONCLUSIONS

Just as internal structures such as genes are central to an understanding of morphological selection and speciation through descent with modification, so also are the genes and nervous system of the behaving organism central to an understanding of behavioral selection by consequences and the development of repertoires. An organism's genes obviously participate in the variation of the characteristics and properties of the organism's behavior. The role of genes is that of a recipe not a destiny, or a set of instructions not a blueprint. Let us focus on the ontogenic level. An organism that by virtue of its genetic endowment has a recipe for a greater supply of uncommitted behavior and a greater susceptibility to reinforcers than other organisms has an adaptive advantage over those other organisms. Changes in an organism's nervous system as a consequence of the organism's experiences with the environment, such as when operant behavior develops, are analogous to mutations in an organism's genetic endowment from parents to offspring. Language is responsible for the replication of certain cultural practices at the cultural level in humans. The changes in the human nervous system that resulted in the potential for operant control over verbal behavior are particularly noteworthy because so much that is uniquely human follows from those changes. Nevertheless, an organism that didn't behave with respect to the environment didn't survive, and it left no descendants in the present world about which we are concerned. Both an organism's genes and its nervous system make adaptive behavior possible, and they are themselves evolved aspects of life.

Explanations of behavior in traditional psychology typically appeal to various acts, states, mechanisms, and processes from a nonbehavioral domain - typically mental or cognitive - as antecedent, mechanistic causes, as either initiating or mediating organismic causes in the style of mediational S-O-R neobehaviorism. Because of historical and cultural traditions, these organismic causes were considered unobservable, but researchers and theorists rendered them scientifically respectable by designating them as "hypothetical constructs" and operationally defining them. The thesis of selection offers an entirely different approach to understanding the causes of behavior. This approach is based on naturalistic concepts from biology: adaptation, selection, contingencies, and so on. This alternative approach ultimately yields a more effective understanding of behavior.

At present, researchers and theorists are debating several matters relating to selection. One is the unit of selection. Is the unit the gene itself, the individual organism, or the entire group of organisms? In regard to selection at the cultural level, is it useful to consider that small patterns of social organization and interaction ("memes") are replicated across a culture, much as small aspects of morphology are replicated across a population of organisms? Little consensus exists in these debates, which in science generally implies the way is open for creative thought in resolving the debates.

In conclusion, we see that for humans, behavioral selection by consequences operates across three levels: phylogenic, ontogenic, and cultural. The process consists of (a) variation; (b) differential interaction with the environment; and (c) differential replication of the behavior, through transmission to and expression in the future. Across the three levels, there are individuals who engage in varying (a) innate responses, (b) emitted responses, and (c) cultural practices. Across the three levels, the nature of the interaction involves (a) survival of the species, (b) reinforcement, and (c) problem solving of the culture, ultimately leading to its overall welfare and survival. Across the three levels, the differential replication of behavior is accomplished through (a) genetics, (b) modifications in the nervous system, and (c) language. The process is cyclic and repeats over time, as the environment interacts with the population and the characteristics of that population change in turn. In addition, the environment that does the selecting may also change. Innate behavior and operant responses contribute to an individual's behavioral fitness, depending on how readily they contribute to adaptation to the contingencies in a given environment. Likewise, cultural practices contribute to a culture's fitness, depending on how readily the practices contribute to adaptation to the contingencies in a given environment, particularly concerning survival. If the environment changes, a formerly fit innate response, operant response, or cultural practice may no longer be of service to the species, individual, or culture. Indeed, the formerly fit response may actually work against the welfare or survival of the species, individual, or culture. Thus, behavioral fitness may be understood as conditional on the circumstances that prevail in a given environment at a given time, just as is morphological fitness. Behavior is neither good nor bad in an absolute sense, nor does it show purposive design. In addition, there may be intermingling of the contingencies across the three levels. An organism might behave aggressively as a result of phylogenic, ontogenic, or cultural influences. Domesticated animals that pull a plow or a cart or that herd livestock exhibit a complex set of influences across phylogenic and ontogenic levels. The entire approach makes psychology, as a science of behavior, an intrinsic part of biology, by virtue of the common reliance on selection by consequences as a causal mode.

Important words and phrases: Evolution, selection by consequences, natural selection, sexual selection, artificial selection, variation, differential interaction, differential replication, transmission, expression, traits, descent with modification, lineage, mutations, fitness, Lamarckism, phylogenic level, elicitation, released forms of species-specific behavior, ontogenic level, operants, conditioned respondents, cultural level, cultural practices, species, reinforcement, survival, extinction, morphology, shaping, contingency, contingency of reinforcement, contingency of survival, gene, behavioral genetics, ethology, behavior analysis, cultural anthropology, selection of, selection for.

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